CHROMOSOME STRUCTURE AND BEHAVIOR IN MITOSIS AND MEIOSIS

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With plates 161–164

A STUDY of chromosome structure and behavior at mitosis and meiosis has been made in order to compare the two types of divisions and to aid in the analysis of the mechanism of meiosis. This work is based on a comparison of chromosome lengths at different stages in the mitotic and meiotic cycles, and the relation of these changes to the internal structure of the chromosomes.

The chromosome cycle in mitosis and meiosis has been studied in *Tradescantia paludosa, Vicia faba, Lilium regale,* and in *Allium Cepa.* The length of the chromosomes at various stages was also obtained in somatic cells of *Trillium grandiflorum,* and some work was done on the meiotic divisions in *Secale cereale* and in *Zea mays.* Recent advances in cytological technique have made possible a fairly accurate study of the length and structure of the chromosomes at various stages in the mitotic and meiotic cycles.

The meiotic figures were obtained from microsporocytes which were smeared on a dry slide, pretreated with 30 percent alcohol containing about six drops of ammonia water per 50 cc., and fixed and stained with aceto-carmine, or fixed in Flemming's solutions and stained with crystal violet iodine. The best preparations of somatic divisions were obtained from young microspores. After smearing on a dry slide they were pretreated with the alcohol ammonia for about a minute and then fixed either in aceto-carmine or Flemming's solution. Root tips were fixed for 12 to 15 hours in a mixture of absolute alcohol (70 cc.) and glacial acetic acid (30 cc.) and then macerated in a drop of aceto-carmine. In all cases the aceto-carmine smears were heated to clear the cytoplasm and the cover glass pressed to flatten the cells. The preparations were then sealed or made permanent by McClintock's method. The aceto-carmine preparations showed almost as much detail of structure as those fixed in Flemming's solution, and since the cells fixed in aceto-carmine could be flattened, these preparations were used in measuring chromosome lengths and were photographed to illustrate the various stages in mitotic and meiotic cycles.

THE MITOTIC CYCLE IN TRADESCANTIA MICROSPORES

At anaphase of the second meiotic division each chromosome consists of two spiral chromatids. When the chromosomes pass into the resting stage the chromonemata tend to uncoil and form a loose spiral structure which completely fills the nucleus. Well fixed preparations show distinct chromatic threads loosely coiled in the resting nucleus rather than a reticulate network (Plate 161, photo 1). At early prophase the nucleus enlarges and the spiral chromosomes are more easily observed (Plate 161, photo 2). The chromatids of each chromosome are so clearly associated that the doubleness is hardly discernible, a condition also observed by Kuwada and Nakamura (1935). As the prophase continues the coils tend to straighten out and at the same time there is evidence of a new coiling in the closely associated chromatids (Plate 161, photo 3). At this stage there is little evidence of the double thread structure of the chromosomes even though they appear to be two-parted at the preceding anaphase. When the old coils are straightened out so that the spireme thread can be followed at all loci, there is clear evidence of a longitudinal split and each chromatid is independently coiled (Plate 161, photo. 4). These new coils apparently shorten the chromosomes and draw out the old coils persisting from the previous anaphase of the second meiotic division. The chromosomes continue to shorten during anaphase and the chromatids become thicker and more clearly separated (Plate 161, photo. 5). There is some tendency for the two chromatids of a chromosome to be twisted about each other, but at most only two or three twists occur. These are usually eliminated by metaphase although overlaps and an occasional twist is found at this stage (Plate 161, photo. 7).

In preparations fixed without pretreatment, there is little or no evidence of the coiled chromosome structure at metaphase (Plate 161, photo. 6). The two chromatids of each chromosome usually can be identified although with certain types of fixation and staining the metaphase chromosomes appear as single rods. After effective pretreatment of the microspores the coiled chromatids can be seen at early metaphase and at anaphase (Plate 161, photos. 7, 8, 9). The diameter of the chromatid is so near the limit of microscopic resolution that it has not been possible to determine the direction of coiling, nor can the number of coils be determined accurately, but there appear to be about twenty-five coils in each chromatid (Plate 161, photo. 8). When the chromatids are twisted about each other at early metaphase the chromosome appears to be constricted at the point of overlap as is shown in the chromosome at the right in photo. 7 of Plate 161.

Each chromatid at metaphase and at anaphase usually appears to consist of a single coil, but there is some evidence that these chromatids contain two threads which are coiled together. In the first meiotic division the major coils are so closely associated that they appear as a single coil unless lightly stained, but at late metaphase the two coils separate and lie parallel. In the somatic chromosomes the two coiled threads in the anaphase chromosome do not separate enough to appear as two parallel coils, and the diameter of the chromatids is too small to permit the direct observation of two chromatic threads coiled together, but there is apparently a tendency for the two coils to separate so that when a twist occurs in an anaphase chromosome there is a constricted locus at the twist (Plate 161, photo. 9). Such constrictions may be observed even in the chromatids at early metaphase (Plate 161, photo. 8).

The chromosomes at late telophase appear so compact that little detail in structure can be observed, but as they elongate at later stages the coiled chromonemata expand and irregular coils and corrugations may be observed. The chromaticity of the chromosomes is reduced so that it is not possible to follow the coiling in any single chromosome and the entire nucleus is filled with loosely coiled chromonemata in the resting stage.

The somatic divisions observed in aceto-carmine preparations of root tips did not show the detail of the structure found in the microspores, but the general behavior is the same, except that the root tip chromosomes are longer than those of the microspore at the metaphase stage of division.

THE MITOTIC AND MEIOTIC CYCLES IN VICIA FABA

The early prophase stages in root tips of *Vicia faba* show the irregular spiral chromonemata. At this stage the chromatic threads appear to be single at most loci. As the spireme threads tend to straighten their dual nature is easily observed at all points (Plate 162, photo. 1). The chromatids are twisted about each other to a greater extent than is found in *Tradescantia*, and as many as five or six twists may be observed in a single chromosome. The chromatids appear to be independently coiled in small loose spirals at this stage. During later development the chromatids thicken and shorten until metaphase, but we have been unable to observe the internal structure at this stage. The anaphase chromosomes seem to show a double spiral structure (Plate 162, photo. 2), but not as clearly as in the figures published by Sharp (1929).

The prophase stages in the microspore nucleus are more difficult to follow, presumably because of the rather thick wall of the microspore,

and the metaphase and anaphase stages show little or no detail of structure (Plate 162, photos. 6, 7, 8). The lengths of the prophase spireme and of the metaphase and anaphase chromosomes can be obtained, and it was found that the microspore chromosomes are shorter than those of the root tip cells at metaphase and anaphase.

The early meiotic stages were not studied in detail, but measurements were made of the pachytene spireme. There is a great reduction in chromosome length between pachytene and the first meiotic metaphase. The meiotic chromosomes at the first meiotic metaphase are even shorter than the metaphase chromosomes of the microspore mitosis. The long "m" chromosome has an average chiasma frequency of about 6 while the average chiasma frequency of the short "m" chromosomes is about 3 (Plate 162, photo. 3). The chromonemata are coiled in major spirals at metaphase and at anaphase (Plate 162, photo. 4). A description of these coils will be presented in a later paper. At late anaphase the meiotic chromosomes contract considerably (Plate 162, photo. 5). During the second meiotic division the major coils may persist, but frequently they are completely eliminated at this time and the chromosomes at anaphase appear as straight rods.

THE MITOTIC AND MEIOTIC CYCLE IN LILIUM REGALE

The root tip preparations of *L. regale* showed only the more general features of chromosome behavior. The prophase and metaphase stages were clear enough to provide measurements of the mitotic chromosomes (Plate 163, photos. 3 and 4).

The pachytene stages of meiosis showed the association of chromomeres as described by Belling and others. The pachytene chromosomes are much thinner and longer than the chromosomes of the "spireme" in root tip cells (Plate 163, photo. 1). The chromosomes of the first meiotic division are much shorter than the somatic chromosomes (Plate 163, photo. 2). There is clear evidence of major coils in these meiotic chromosomes and the average chiasma frequency is about 3 per bivalent.

The microspores did not provide good preparations for prophase stages, but Dr. W. S. Flory obtained metaphase figures in another species which could be measured.

OBSERVATIONS OF CHROMOSOMES IN TRILLIUM, ZEA, ALLIUM AND SECALE

Root tip preparations of *Trillium grandiflorum* provided prophase and metaphase figures which could be measured for comparison with corresponding stages in other genera. The prophase spireme in somatic cells is not so clearly split as is the case in *Tradescantia* and *Vicia* (Plate

163, photo. 5). The contraction of the chromosomes from the prophase spireme to metaphase is less than it is in the other genera which have been studied, and the metaphase chromosomes are very long (Plate 163, photo. 6). There is some twisting of sister chromatids about each other even at metaphase.

We have made no detailed study of Zea chromosomes, but McClintock's figures (1933) show about an 11 to 1 reduction in length between pachytene and the first meiotic metaphase, and according to McClintock (personal communication) the ratio may be as great as 15 to 1.

The meiotic cycle in *Allium Cepa* is especially clear for a study of chromosome contraction from pachytene to metaphase (Plate 164, photos. 3–6). The association of chromomeres can be observed at pachytene and the number of nodes is greatly reduced from early diplotene to metaphase. Most of these points of contact seem to be twists or overlaps.

A few measurements of mitotic and meiotic chromosomes were obtained from *Secale cereale*. The structure of the meiotic chromosomes has been described in some detail in an earlier paper (Sax, 1930).

CHROMOSOME LENGTH AT VARIOUS STAGES IN MITOSIS AND MEIOSIS

We have obtained measurements of chromosome lengths at prophase and metaphase in mitotic and meiotic cells of the various species examined. The prophase measurements of root tip cells were made after the old coils were straightened out and the new coils were started, the so-called spireme stage of mitosis. The cells were flattened so that most of the spireme could be drawn in two focal levels. The measurements of the chromosomes were made from camera lucida drawings, and no attempt was made to determine the additional length caused by foreshortening of threads passing through several focal levels. The lengths of the pachytene chromosomes were easier to obtain, but even these are only approximate. The meiotic chromosomes at metaphase form loops between chiasmata and we have tried to include these in our measurements of Vicia and Lilium chromosomes. The anaphase chromosomes in both mitosis and meiosis are essentially the same length as the metaphase chromosomes in some species so that anaphase figures were occasionally included in determinations of metaphase lengths. In view of the technical difficulties involved in determining comparable stages and in obtaining the prophase measurements, the results are only approximate, but the differences in chromosome contraction in mitosis and meiosis are so consistent that they must be of some significance. The data obtained are shown in Table I.

TABLE I

Average chromosome length in microns at prophase (P) and metaphase (M) in meiotic and somatic divisions. The number (n) of cells measured is indicated.

	Root tip				Meiotic				Microspore			
Species	n	P	n	M	n	P	n	M	n	P	n	M
Vicia faba	4	48	5	13	2	98	2	9	4	36	2	11
Tradescantia sp.	5	56	8	21	3	81	9	9	8	61	8	12
Lilium regale	3	35	2	22	2	83	4	12			1	15
Trillium grandiflorum	1	91	2	40								
Secale cereale	1	37	1	14	1	61	1	8				
Allium Cepa					4	69	1	9				

In every case where meiotic and mitotic prophases are compared the meiotic pachytene chromosomes are much longer than those at the somatic prophase spireme. The ratios range from about 1.4:1 in *Tradescantia* to about 2.4:1 in *Lilium* and the average ratio for all species examined is about 2:1.

The reduction in chromosome length from prophase to metaphase is much greater in meiosis than in mitosis. The chromosomes at pachytene are from 7 to 11 times as long as the chromosomes at meiotic metaphase and the ratio may be even more extreme in certain species. In root tip cells the prophase chromosomes are shorter, but the metaphase chromosomes are longer than the corresponding stages of meiosis. Consequently the reduction in chromosome length from prophase to metaphase is much less in root tip cells, ranging from less than 2:1 in *Lilium* to about 4:1 in *Vicia*.

The metaphase chromosomes of the microspore are shorter than those of the root tip cells, but longer than the meiotic chromosomes at first metaphase. The technical difficulties in measuring microspore chromosomes probably is responsible for the shorter prophase measurements in microspores of *Vicia* as compared with corresponding stages in root tip cells.

The outstanding feature of these comparisons in chromosome length is the consistent and striking difference in the degree of chromosome contraction in mitosis and meiosis. For the species examined the average degree of chromosome contraction between pachytene and the first meiotic metaphase is about 8.6:1, while for comparable stages in mitosis in root tip cells the ratio is about 2.6:1. In view of the method of calculating chromosome lengths and the greater difficulty in measuring somatic prophases, these average ratios may be considered approximately as 9:1 and 3:1 respectively.

Another bit of evidence should be considered before discussing the possible significance of these observations. In general it is well known

that the meiotic cycle is a leisurely process. The resting stage of the sporocyte may be of short duration in certain species, but the early prophase is prolonged, and in certain conifers the microsporocytes may remain in the early prophase stage for several months (Sax and Sax, 1933). The pachytene stage is prolonged in most species of plants and animals judging by the ease and frequency with which this stage is found. The development from pachytene to metaphase may be rather rapid, but the first metaphase stages, interphase, and second meiotic division are more prolonged. The meiotic cycle from early prophase to tetrad formation in the microsporocytes of *Tradescantia* requires about six days (Sax and Edmonds, 1933). The somatic cycle in the microspore of *Tradescantia* is much more rapid. The prophase stage is not initiated until vacuolation of the microspore cytoplasm, and the development from this stage to the formation of the daughter nuclei occurs in about three days at most. We have no data regarding the time required for the mitotic cycle in root tips of *Tradescantia,* but the duration of mitosis in stamen hairs of *Tradescantia* is less than two hours at normal temperatures (Tischler, 1922). Laughlin (1919) found that the entire mitotic cycle requires only four hours in *Allium Cepa,* at a temperature of 20 degrees C. The duration of the development from the time that a definite spireme can be observed until the separation of sister chromatids appears to be much longer in meiosis than it is in mitosis, and it seems probable that the mitotic cycle is more rapid in root tips than in microspores.

THE MECHANISM OF CHROMOSOME CONTRACTION IN MITOSIS AND MEIOSIS

The chromonemata of mitotic chromosomes in *Tradescantia* are in the form of minor spirals at anaphase in the second meiotic division, the division of the microspore nucleus, and presumably in all other mitotic divisions (Cf. Sharp, 1934). As the chromosomes pass into the resting stage the spirals tend to uncoil and fill the nucleus with loosely and irregularly coiled chromonemata. These old coils are never straightened out before the new coiling is initiated in the prophase for the next division. The new coils contract the chromonemata and apparently aid in drawing out most of the old spirals persisting from the previous division. At this point the chromosomes are in the typical "spireme" stage and their lengths can be measured approximately. The new coiling can be observed during the later prophase stages, and at metaphase there are about 20 to 25 minor spirals in each chromosome. The microspore chromonemata are compactly coiled at metaphase. Judging from the

relative lengths of the metaphase chromosomes in microspores and root tips, the chromonemata of the latter are not so tightly coiled (Cf. Sharp, 1934). In general the development of the minor spirals reduces the chromosome length about 70 percent between the prophase spireme and metaphase in root tip cells, and even more in microspore cells. At no period in the mitotic cycle are the chromosomes uncoiled completely; the spirals from the preceding division persist until the new coiling begins at early prophase. Observations and measurements in several different genera seem to indicate that this behavior is of general occurrence in the somatic cycle of cell division (Cf. Kuwada and Nakamura, 1935).

The chromosomes of the meiotic prophase appear to be free from spirals persisting from the previous mitotic anaphase, and if remnant spirals occur they are so nearly straightened out that they can hardly be recognized as spiral structures at pachytene. There is a great amount of chromosome contraction between pachytene and the first meiotic metaphase in *Vicia, Tradescantia, Lilium, Trillium, Secale, Allium* and other genera. Belling (1928) found a 10:1 reduction in chromosome length in *Lilium* and Dark (1934) found an 11:1 reduction in *Bellevalia*. The average reduction in chromosome length between pachytene and metaphase in the genera which we have examined is about 9:1. An examination of published drawings of these stages in other genera of plants with large chromosomes indicates that a similar degree of chromosome contraction is of general occurrence.

The paired chromosomes at early pachytene are very slender, and even at late pachytene the diameter of the chromonemata is much less than it is at corresponding stages in mitosis. During the contraction between pachytene and metaphase the chromonemata become coiled in major spirals. The two chromatids of each chromosome are coiled together in single spirals at early metaphase in *Tradescantia* (Sax and Humphrey, 1934), *Secale* (Sax, 1930), *Rhoeo* (Sax, 1935) and *Vicia*, but two parallel coiled chromatids are found at this stage in *Gasteria* (Taylor, 1931), *Trillium* (Huskins and Smith, 1935) and *Fritillaria* (Darlington, 1935). These major coils are much wider and fewer in number than the minor spirals of the somatic chromosomes. In *Tradescantia* there are 5 to 6 major coils in each chromosome at meiosis, as compared with 20–25 coils in somatic chromosomes, and the gyres of the major coils are about twice as wide as those of the minor coils. Darlington (1935) finds from 8 to 15 major spirals in the meiotic chromosomes of *Fritillaria* and about 80 minor coils in the somatic chromosomes.

Minor spirals within the major coils have been observed in *Tradescantia* (Fujii, 1926; Ishii, 1931; Kuwada, 1932; Kuwada and Naka-

mura, 1933; Kato, 1934); in *Hosta* (Ishii, 1931); in *Sagittaria* and *Lilium* (Shinke, 1934), and in *Trillium* (Matsuura, 1934). (For these literature citations see Kato and Iwata (1935), who also describe the spiral within spiral structure of the meiotic chromosomes of *Lilium*.) Our observations and measurements of chromosome length in mitosis and meiosis seem to show that the relations of the major and minor coils differ in different genera. In *Tradescantia* the minor coils seem to be well established at early metaphase so that the separation of the major coils at late metaphase is associated with little change in the coiled chromatids. There is, however, some reduction in the width of gyres between early metaphase and anaphase, which can be attributed to the continuation of minor coiling. If the minor coils are well developed at metaphase the length of the meiotic chromonema of the major coil should be about the same at the somatic metaphase chromosomes. We have made wire models simulating the major coils in order to estimate the degree of contraction caused by the major spirals. The coiling is responsible for about a two-thirds reduction in length, so that the meiotic chromonemata of *Tradescantia*, including only the major coils, are about 27 microns long, as compared with an average length of 21 microns for the somatic chromosomes. If only coiling is responsible for chromosome contraction in *Tradescantia* the minor coils at meiotic metaphase are nearly as well developed as they are in root tip chromosomes.

In *Secale* we find a different relation between the major and minor coils at meiosis (Sax, 1930). The two chromatids of each homologue are coiled together in a single spiral at early metaphase, but at late metaphase the major spirals tend to straighten out and the chromatids separate with no elongation of the meiotic chromosomes. The average length of these coiled chromonemata at early metaphase is estimated to be about 24 microns, but after the major coils are reduced at late metaphase the chromosome length is about 8 microns. The somatic chromosomes at metaphase have an average length of about 14 microns. Apparently the minor coils are not well developed at early metaphase, but are formed during metaphase and are effective in reducing the major spirals. The relations of the major and minor spirals in *Vicia*, *Lilium* and *Rhoeo* are more or less intermediate as compared with the conditions found in *Tradescantia* and *Secale*.

If chromosome contraction is effected only by coiling of the chromonemata we would expect that the degree of reduction in length between pachytene and metaphase would be correlated with the relation between major and minor coiling. There does seem to be some correlation in certain genera. In *Tradescantia* where both major and minor coils occur

together at meiotic metaphase, the ratio of chromosome length at pachytene and meiotic metaphase is about 9:1. All of this chromosome contraction might be attributed to major and minor coiling. In *Rhoeo* and *Zea*, however, the pachytene metaphase ratio may exceed 15:1, although there are no apparent major spirals in the meiotic chromosomes of *Zea*, and in *Rhoeo* the minor spirals appear to be most effective in chromosome contraction during late metaphase as the major spirals are reduced (Sax, 1935). Apparently there may be some linear contraction of the chromonema without coiling as Belling (1928) has suggested.

The major spirals may be observed at the second meiotic division, as is usually or always the case in *Gasteria, Trillium, Sagittaria* and *Fritillaria*, or only minor spirals may occur as is the case in *Tradescantia, Rhoeo*, and presumably in all genera in which the second meiotic division chromosomes resemble those of mitosis. In *Lilium* and in *Vicia* some chromosomes show major spirals and others only minor spirals at the second meiotic division. The nature of the coiling at this division appears to be associated to some degree with the length of the interphase.

The outstanding features of meiosis in relation to chromosome contraction are, (1) the almost complete elimination of the coils of the preceding anaphase chromosome at the pachytene spireme, (2) the great reduction in chromosome length between pachytene and metaphase, and (3) the occurrence of major spirals.

THE TIME OF THE CHROMOSOME DUPLICATION

The anaphase chromosomes at mitosis have been described as two parted in *Tradescantia* (Kaufmann, 1926); *Trillium, Allium, Tradescantia, Vicia, Podophyllum* (Sharp, 1929; Telezynski, 1930); *Galtonia* (Smith, 1932); *Scilla* (Hoare, 1934); *Narcissus* (Hedayetullah, 1931); *Drosophila* (Kaufmann, 1934) while four parted chromosomes at late anaphase or telophase have been described in *Tradescantia* (Nebel, 1932) and *Paeonia, Allium* and *Tulipa* (Stebbins, 1935). Two coiled chromatids in the anaphase chromosomes of the second meiotic division have been described in *Gasteria* (Taylor, 1929, 1931), *Galtonia* (Smith, 1932), *Allium* (Koshy, 1934), *Scilla* (Hoare, 1934), *Trillium* (Huskins and Smith, 1935), *Rhoeo* (Sax, 1935) and *Tradescantia* (Nebel, 1932; Kuwada and Nakamura, 1935). The anaphase chromonemata at mitosis are described as longitudinally single structures by Belar (1928), Darlington (1932, 1935) and Belling (1933), although Belar shows clearly the longitudinal split at late anaphase in *Aulacantha*.

The anaphase chromosomes of the second meiotic division in *Tradescantia* have been described as single structures (Sax and Humphrey,

1934), but further study tends to confirm the interpretation of Kuwada and Nakamura, who present photographic illustrations which show the dual nature of these anaphase chromosomes. We can observe both in the second meiotic anaphase and in the anaphase chromosomes of the microspore division, some evidence of two closely associated coiled chromatids and the constrictions apparently produced by the twisting of the partially separated spirals. The experiments conducted by Riley (Cytologia, in press) indicate that the split chromosome behaves as a unit in response to X-ray treatment, since the microspore nuclei rayed during the resting stage show only chromosome breaks at metaphase. X-ray treatment at the resting stage of microspore nuclei in *Trillium* produces only chromatid breaks at metaphase, indicating that the chromosomes are effectively split when they go into the resting stage (Huskins and Hunter, 1935). The differences in the response to X-ray treatment in these two genera may be caused by the degree of separation of the sister chromatids. In *Trillium* the chromatids are well separated at diplotene and form more or less independent major spirals at early metaphase, while in *Tradescantia* the two chromatids of each homologue are closely associated at early metaphase of the first meiotic division. A corresponding difference in the relations of the chromatids may exist during the later stages of meiosis and early microspore development.

The available evidence seems to show that the chromonemata are longitudinally split when they enter the resting stage, and they may be four parted as indicated by the careful work of Nebel and Stebbins. If they are four parted at this stage the split chromatids may behave as units during the next mitotic cycle, so that the chromosomes may be considered as composed of two chromatids when they enter the resting stage (cf. Nebel, 1933).

The time at which chromosome duplication is initiated is a question on which there is considerable difference of opinion. Some investigators believe that it occurs at very early prophase while others find the split at late prophase, metaphase or even at anaphase or telophase. We are inclined to associate chromonema coiling with the longitudinal split of the chromosome. The chromosomes are considered as two parted when they enter the resting stage. In mitosis the two chromatids are coiled together in loose spirals at the beginning of prophase. At early prophase each of the two chromatids is longitudinally split. This split causes each split chromatid to coil independently. This coiling pulls out the remnant coils of the previous anaphase and causes the chromatids to separate so that two more or less parallel strands are observed at the spireme stage. These shorten by coiling, separate at anaphase, and each anaphase chromosome contains two closely associated spiral threads.

The leptotene threads at meiosis are also split, as observed by McClung (1928) and Robertson (1931), although they usually appear to be single. The threads pair at pachytene, and at late pachytene each chromatid splits and the coiling of the chromonemata begins as in mitosis. At diplotene the homologous chromosomes separate except at chiasmata or where twists occur. The minor spirals at meiosis involve only two strands or half-chromatids, as in mitosis. The minor spirals appear to begin development before the major spirals, but they may develop so slowly that they continue to coil, or at least contract, after the major coils are established at early metaphase in certain species. The meiotic bivalent is an eight parted structure as described in *Tradescantia* (Nebel, 1932), in *Trillium* (Huskins and Smith, 1935) and as we have observed in *Tradescantia* (from a preparation made by Dr. Dermen).

The chromosomes separate at anaphase, the two chromatids of each chromosome appear as parallel coils, but the "tertiary split" can not be seen. The interphase is brief and even the major coils may persist at the second division. There is apparently no true resting stage at interphase and the chromosomes pass to the second metaphase as four parted structures. At second anaphase each chromosome contains two coiled chromatids as a result of the split which occurred at late pachytene or early diplotene. The number of strands and time of splitting in any one of the 2n chromosomes is essentially the same in both the mitotic and meiotic cycles.

THE MECHANISM OF MEIOSIS

According to Darlington (1932 "meiosis differs from mitosis in the nucleus entering prophase before the chromosomes divide instead of after they divide. The "precocity theory" is based on the assumption that there is a curtailed resting stage or earlier prophase and that the leptotene chromosomes are single. Evidence from many sources indicates that the chromosomes contain at least two coiled chromatids when they enter the resting stage in the mitotic cycle and at the completion of meiosis. There is little reason for assuming that the last premeiotic division differs from other mitoses.

There is good evidence that the meiotic cycle is a much more leisurely process than the mitotic cycle. This evidence, together with the observations on chromosome length at prophase in mitosis and meiosis, seems to indicate that meiosis is associated with a retardation in cellular activity rather than precocity in development (Cf. Stebbins, 1935). The prolongation of prophase at meiosis is associated with the straightening out of the old spirals of the preceding anaphase before the new coiling begins. The two chromatids of each leptotene chromosome are so closely asso-

ciated that they appear as a single thread. At mitosis there often is a tendency for homologous chromosomes to be associated in pairs, but intimate gene by gene pairing is inhibited by the coiled structure of the chromonemata. As the remnant coils begin to straighten out the chromatids are split and the new coiling begins so that the chromonemata are always coiled during the mitotic cycle. In meiosis, however, no coils, or at least only very loose remnant spirals, are found at prophase, and an intimate association of homologous chromosomes is effected. The new split occurs in each chromatid at late pachytene, coiling begins, and homologous chromosomes begin to separate. At this stage of chromosome development, in both mitosis and meiosis, each chromosome (2n) contains four chromatids and there is no longer any strong affinity between homologues. In meiosis the homologous chromosomes usually appear to be held together by chiasmata, although other factors appear to be effective in the meiotic association of chromosomes in certain cases. At interphase the pairs of "sister" chromatids separate except at the fiber attachment, and at second metaphase they again become closely associated. The anaphase chromosomes pass into the resting stage as double spirals as in mitosis. The prolongation of the mitotic cycle in the microspore suggests that the retardation of meiosis tends to persist at the subsequent mitosis so that the microspore chromosomes are more compactly coiled than in root tip cells, but the retardation at early prophase is not sufficient to effect chromosome pairing even in autotetraploids.

The retardation theory of meiosis is in accord with the numerous observations that the anaphase chromosomes pass into the resting stage as two parted (or four parted) structures, and with the fact that the meiotic prophase chromosomes are much longer than those of the mitotic spireme. The primary difference between mitosis and meiosis is the longer prophase in meiosis which enables the residual coils of the chromonemata to straighten out and permit the homologous chromosomes to become intimately associated in pairs before the chromatids split and coil.

SUMMARY

A study of chromosome structure and behavior at mitosis and meiosis has been made in *Tradescantia*, *Vicia*, *Lilium*, *Secale*, and other genera.

The somatic chromosomes at the resting stage are in the form of loose spirals. At prophase the chromonemata form new coils which appear as the remnant coils are straightened out. The contraction of the chromosomes between prophase and metaphase is effected by coiling of the chromonemata. The average reduction in length of the chromosomes

between the "spireme" stage and metaphase is about 3:1 in the root tip cells of the species examined, and may be greater in microspores. As the chromosomes enter the resting stage the chromonemata tend to uncoil filling the resting nucleus with loose, irregular spirals. Thus the chromonemata are coiled at all stages in the mitotic cycle.

The chromosomes at meiotic prophase are practically free from remnant coils and the new coils do not appear until late pachytene. The chromosomes at meiotic prophase are about twice as long as those of the mitotic prophase. The average reduction in chromosome length between pachytene and meiotic metaphase is about 9:1. This reduction in length may be effected by linear contraction of the gene string, and by major and minor coiling of the chromonemata. The relation of these factors in chromosome contraction may differ in different genera.

A theory of the mechanism of meiosis has been proposed, based on the comparison of chromosome behavior in mitosis and meiosis, and the comparative duration of the mitotic and meiotic cycles. The chromonemata of mitotic chromosomes are in the form of spirals at all periods of the chromosome cycle and this coiling prevents any intimate association of homologous chromosomes. At prophase of meiosis the chromonemata are relatively free from coils and homologous chromosomes can become closely paired before the new coiling is initiated. The retardation theory of meiosis is in accord with the recent evidence regarding the time of chromosome duplication.

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DESCRIPTION OF PLATES

PLATE 161

Photographs of Tradescantia microspores fixed and stained in aceto-carmine after pretreatment with ammonia alcohol. Magnification × 1200 except photo. 8 which is × 2000.

Photo. 1. Resting stage, nucleus filled with loose spiral chromonemata.
Photo. 2 and 3. Early prophase with remnant spirals from preceding anaphase.
Photo. 4. Prophase spireme with most of the remnant coils removed and the new spirals appearing in each chromatid.
Photo. 5. Late prophase after the chromatids have contracted and more clearly separated.
Photo. 6. The chromosomes at metaphase fixed without effective pretreatment.
Photo. 7. Early metaphase showing the coiled chromonemata in each chromosome and partial twisting of chromosomes about each other.
Photo. 8. Early metaphase showing approximate number of coils, and twists in chromatids.
Photo. 9. Anaphase chromosomes with two coiled chromatids in each chromosome.

PLATE 162

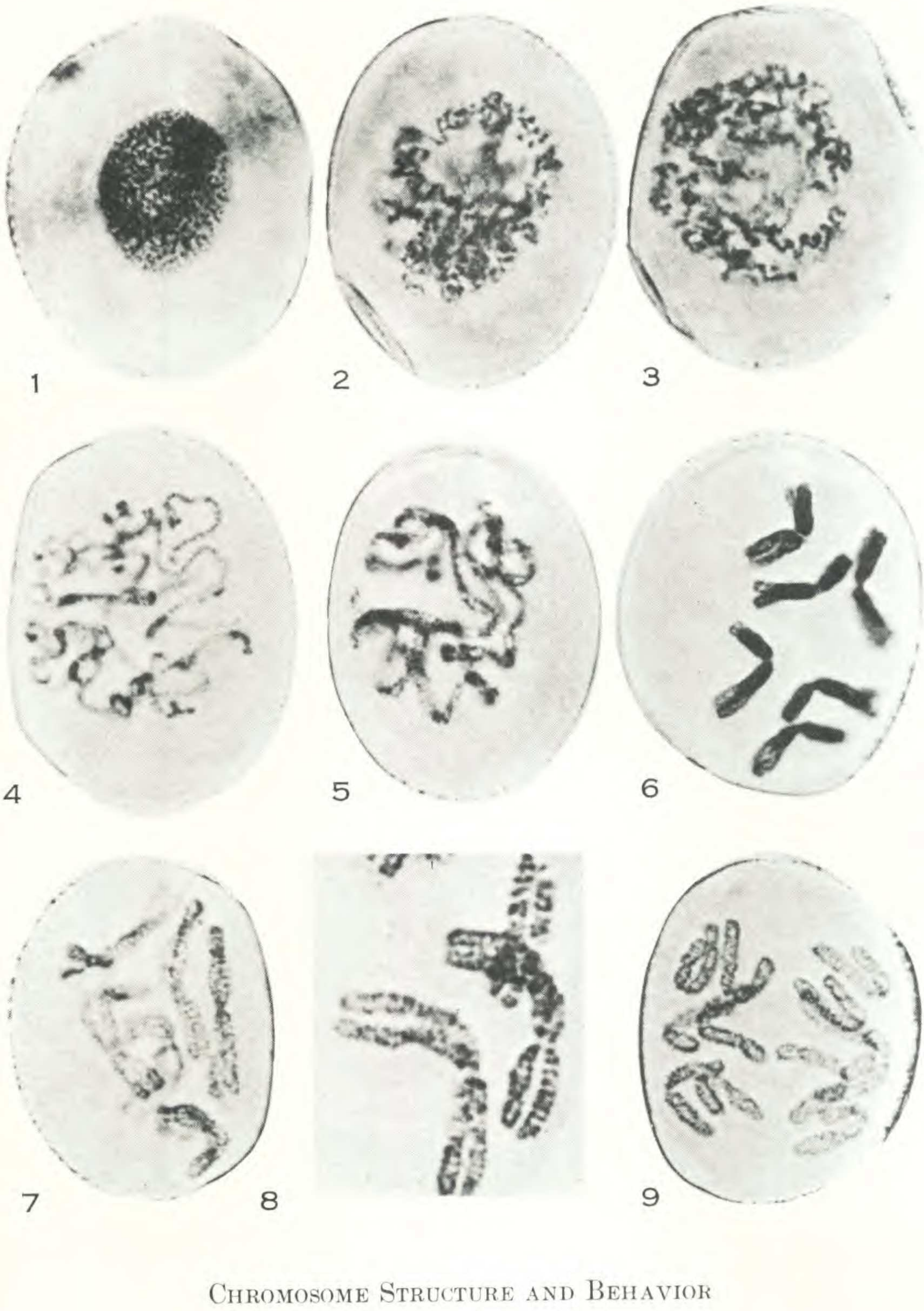
Photographs of mitotic and meiotic chromosomes of *Vicia faba*. Aceto-carmine preparations. Magnification × 1200.

Photo. 1. Prophase spireme of root tip cell.
Photo. 2. Anaphase from root tip chromosomes showing secondary constrictions in the "m" chromosomes, and some evidence of internal spirals.
Photo. 3. Meiotic metaphase showing distribution of chiasmata.
Photo. 4. Meiotic anaphase showing major coils.
Photo. 5. Meiotic telophase showing extreme chromosome contraction.
Photo. 6. Prophase of microspore division.
Photos. 7 and 8. Anaphase chromosomes of the microspore division.

PLATE 163

Photographs of mitotic and meiotic cells from aceto-carmine preparations. Magnification × 800.

Photo. 1. Meiotic pachytene in *Lilium regale*.
Photo. 2. Meiotic metaphase in *Lilium regale*.



CHROMOSOME STRUCTURE AND BEHAVIOR

THE HELIOTYPE CORP. BOSTON